New palaeontological studies on the Chapelcorner Fish Bed (Upper Eocene, Isle of Wight)

J. Gaudant¹ and W. J. Quayle²

¹ 17 Rue du Docteur Magnan, 75013 Paris (France)

² 51 Whites Road, Bitterne, Southampton SO2 7NR

Summary

Recent excavations in the Chapelcorner Fish Bed (Osborne beds, Upper Eocene) of the Isle of Wight have yielded new specimens of crustaceans and fishes. A more complete description of the prawn *Propalaemon osborniensis* Woodward is given while it is suggested that the specimens previously referred to *P. minor* Woodward are really young of *P. osborniensis* Woodward. Three fish species have also been identified. The most abundant is a clupeid originally described as *Clupea vectensis* Newton; the new genus *Vectichthys* is created for it. The second is a relatively scarce gobiid which resembles *Pomatoschistus* (?) bleicheri (Sauvage), from the Lower Oligocene of Alsace. Isolated scales and vertebrae of a species of amiid have also been found.

Prawns and fishes from the Chapelcorner Fish Bed suggest brackish water conditions, and less explicitly that the climate was tropical to subtropical, during the deposition of the fossiliferous clay.

Introduction

The occurrence of fossil fishes and prawns in the Osborne beds of the Isle of Wight was first noted by Colenutt (1888). The fishes were initially studied by Newton (1889), who erected the species *Clupea vectensis*, subsequently transferred to the genus *Diplomystus* Cope by A. S. Woodward (1901). Newton (1899) also distinguished two species among the amiid remains found in the Osborne beds. Moreover, H. Woodward (1903) described two new species of prawns, *Propalaemon osborniensis* and *P. minor*.

All the new material described in this paper comes exclusively from Colenutt's bed 3, better known as the 'Fish Bed', or more precisely as the Chapelcorner Fish Bed (Gamble 1982). Most of it has been found on the shore near Chapelcorner Copse, east of King's Quay Creek, about 3 miles ESE of East Cowes. Some specimens were collected from the shore below Ryde House and Binstead House (west of Ryde) and from Sea View Point (Fig. 1).

The fossils are preserved in a grey-blue shaly clay belonging to the Osborne beds which underlie the Bembridge limestone outcropping in the upper part of the cliff. The stratigraphical position of the Osborne beds has long been controversial, as the Eocene-Oligocene boundary was not clearly defined. Nevertheless, they belong to the Headonian continental stage consid-

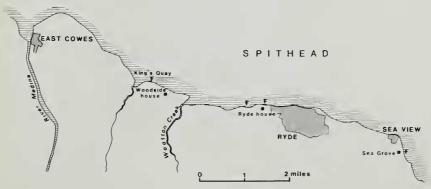


Fig. 1 Map showing the main fossiliferous outcrops of the Chapelcorner Fish Bed.

ered as being the equivalent of Bartonian and Priabonian marine stages. So, their age must be considered as Upper Eocene, the Eocene-Oligocene boundary being placed between the Bembridge marls and the Lower Hamstead beds in the Hampshire basin (Cavelier 1979). Within the lithostratigraphic nomenclature proposed by Insole & Daley (1985) the Chapelcorner Fish Bed is contained within the Fishbourne Member of the Headon Hill Formation, Solent Group. Details of the section may be found in Insole & Daley (1985: 84, fig. 17).

Repositories

Fossils described in this paper are kept in the following museums: British Museum (Natural History), Department of Palaeontology, London (BMNH); British Geological Survey, Keyworth (BGS); Sedgwick Museum, Cambridge (SMC); University of Manchester Museum, Department of Geology (UMMG); and Isle of Wight County Geological Museum, Sandown (IWCGM). All figured specimens are in the BMNH—prefixed by I, In or P—except Fig. 10C.

Explanation of abbreviations used in figures

Ab S	abdominal somite	n.a.PU1 to	neural apophysis of preural
Ang	angular	n.a.PU3	vertebrae
Ant	antennules	n.a.U1	neural apophysis of ural centrum
As	antennular scale	Op	operculum
Che	chela	PHy	parhypural
Chy 2	posterior ceratohyal	Pl	pleopod
Cl	cleithrum	Pmx	premaxilla
d.c.s.	dorsal caudal scute	Pop	preoperculum
Dent	dentary	Psph	parasphenoid
E	eye	PT	post-temporal
Ecpt	ectopterygoid	PU ₁ to PU ₃	preural vertebrae
Enpt	entopterygoid	$PU_1 + U_1$	uro-terminal complex
Ep, Ep 1–3	epurals	Q	quadrate
Fr	frontal	R	rostrum
f.t.	temporal fossa	R br.	branchiostegal ray
h.a.PU2 to	haemal apophysis of preural	SC1	supracleithrum
h.a.PU3	vertebrae	Smx_1, Smx_2	supramaxillary bones
Hmd	hyomandibular	Sop	suboperculum
Hy 1 to Hy 6	hypurals	Sy	symplectic
1	unbranched principal ray of the	T	telson
	caudal fin	U1, U2	ural centra
Iop	interoperculum	Unl to Un3	uroneurals
Iorb.1	lachrymal	Uro	uropod
Mx	maxilla	v.c.s.	ventral caudal scute

Systematic description: Crustaceans

W. J. Quayle

Infraorder CARIDEA Dana, 1852

Family PALAEMONIDAE Rafinesque, 1815

Genus PROPALAEMON Woodward, 1903

Propalaemon osborniensis Woodward, 1903 Figs 2–4

1903 Propalaemon osborniensis H. Woodward: 98; pl. 5, figs 1-4.

1903 Propalaemon minor H. Woodward: 98; pl. 5, figs 5-7.

1925 Propalaemon osborniensis Woodward; Woods: 4; pl. 1, fig. 2.

1925 Propalaemon minor Woodward; Woods: 5.

1929 Propalaemon osborniensis Woodward; Glaessner: 340.

1929 Propalaemon minor Woodward; Glaessner: 340.

LECTOTYPE. Of the original material upon which H. Woodward based his description of *P. osborniensis* only one specimen (BMNH 1n.24494) has been located and is here designated **lectotype**.

MATERIAL. BMNH 1n.24494 (lectotype), 1.4856-7, In.61764-78, In.61687-99; SMC C.23660-1.

H. Woodward based his description of *Propalaemon osborniensis* on 29 specimens collected by Colenutt and Hooley. All the specimens came from the Osborne beds of the Isle of Wight: the majority from Chapelcorner Copse between King's Quay and Wootton Creek. The remainder came from the shore below Ryde House, Binstead House and south-east of Sea View Pier. Unfortunately there is no indication that the specimens in the Sedgwick Museum were included among the original material.

[In a letter to the senior author, Dr G. F. Elliott writes that the late A. G. Davis, who died in 1957, had told him that, when looking for specimens which belonged formerly to Colenutt (who died in 1944), he had succeeded in locating Colenutt's cabinet in Ryde (Isle of Wight). However, the landlord of the house informed Davis that the fossils had been thrown away as they seemed to be devoid of commercial value.]

REMARKS. In his description H. Woodward (1903) divided the prawns into two groups, of large and small individuals respectively. The large specimens (carapace length 20 mm, Fig. 2A) he described as *P. osborniensis*. The smaller ones ('26 mm in length of which the carapace measures 10 mm') he thought could be young forms of *P. osborniensis*, but since there was no positive evidence available, he considered it convenient to treat them as a distinct species, to which he gave the name *P. minor*. Both Woods (1925: 5) and Glaessner (1929: 340) were inclined to agree with this opinion.

Among the recently collected material are specimens equivalent in size to *P. minor* (BMNH In.61692, In.61694, In.61695: Fig. 2C) which however show details of the rostrum, pleopods, abdomen and antennal scale not readily available to H. Woodward and which compare favourably with *P. osborniensis*. *P. minor* Woodward is therefore here considered a junior synonym of *P. osborniensis* Woodward; the latter has been designated by Woods (1925) as the type species of the genus *Propalaemon* Woodward.

Woods (1925) remarked of *P. osborniensis* Woodward that 'the specimens examined by Woodward were very imperfect and owing to subsequent changes in the matrix, have become even more indistinct: at present no other specimens can be obtained and consequently it is not possible to give a diagnosis of the species or to discuss its generic position'. The diagnosis proposed by Glaessner (1969), however, is fundamentally sound. The specimens are preserved in a grey-blue shaly clay and it is evident by comparison with recently-collected material from the type localities that little, if any, change in the matrix of the original material has taken place.

Since the new material shows features not present on the specimens examined by H. Woodward, a revision of the description, incorporating his original observations where appropriate, is given.

DESCRIPTION. The size of the prawns varies from a few millimetres up to 60 mm in overall body length.

The upper margin of the rostrum is lined with six even-sized, sharp, triangular teeth. The first tooth occurs just posterior to the orbit and from there the rostrum (seen to advantage on In.61687 and in In.61766: Fig. 2B) slopes gently upwards as in the Recent forms of *Palaemon*. The underside of the rostrum tapers slightly towards the tip and on In.61766 two teeth can be seen distally. Two specimens (In.61766, In.61770) show that the tip of the rostrum was bifid; the lower member protrudes and is twice the size of the upper.

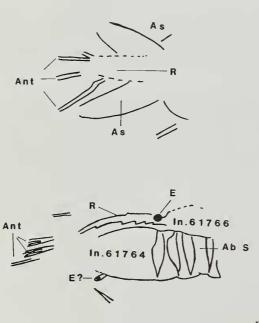
The antennules are three-flagellate. The outer pair are long, whilst the median one, although shorter, extends beyond the tip of the antennular scale (In.61764). The antennar flagella are long, but their full length cannot be seen on any of the specimens examined. On most specimens an antennal scale is present; the outer margin, straight for most of its length, curves inwards at the tip. The inner margin is straight proximally and tapers gradually until the widest part is reached at one-third the length. At this point it curves inwards and the width decreases

to the tip; the edge is 'feathered' with fine setae. The length of the scale on a specimen with a carapace length of 16 mm is 12·5 mm. On In.61764 and In.61692 can be seen what is possibly an antennal scale.

The posterior margin of the carapace is bordered by a ridge; on the branchial region parallel to this ridge there is a line of small, evenly-spaced pits with some isolated pits parallel to them (In.61689).

The uropods are slightly longer than the telson, with the margin of the telson being simple (In.61690: Fig. 3A). The pereiopods as far as preserved are long and slender, the first and second limbs being chelate (In.61765: Fig. 3B); the chelae of the second pereiopods are three times the length of the chelae of the first pereiopods. The distal joint of the third maxilliped is acuminate and has a line of pores running along the outer margin (In.61691).

According to H. Woodward (1903), the pleopods of one specimen (the lectotype In.24494) were said to be 12 mm in length and the ambulatory legs 25 mm. Two specimens, In.24494 and 1.4856, show that the pleuron of the second abdominal somite overlaps that of the first and third pleura. A single spine on the hepatic region could be observed (Woodward 1903: figs 2, 4), and among the recently collected material In.61689 shows the base of what was probably a spine in this area. Owing to the way the material is preserved, no further details of the abdomen could be observed.



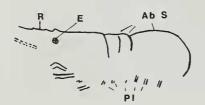


Fig. 2 Propalaemon osborniensis Woodward. A, anterior portion showing antennules and antennular scale. In.61688 preserved in a dorsoventral position (×5·5). B, In.61764 preserved in a dorsoventral position showing antennules, eye, and somites. In.61766 lying alongside preserved in a lateral position, showing upper margin of rostrum (both × 2·4). C, In.61695 (×5·5) preserved in left lateral view







DISCUSSION. H. Woodward (1903) stated 'the bifid flagella of the inner antennae are preserved in fig. 1 and fig. 2'. These are possibly the inner and outer flagella while the shorter median one is hidden between them. In the new material this smaller flagellum is present on two specimens (In.61688, In.61764: Fig. 2A, B) which are preserved crushed in a dorsoventral position rather than in the more customary lateral attitude. It is possible that only specimens in the latter position were available to H. Woodward.

It appears that the carapace size quoted by H. Woodward included the rostrum (1903: fig. 1, carapace 20 mm). In the above description the carapace length was measured from the hinder margin of the orbit to the posterior margin.

RELATIONSHIPS. Houša (1956) described a new genus, Bechleja, but no doubt owing to the state of preservation of available material much information appears to be lacking from the comparisons he made with other known fossil palaemonid prawns. Feldmann et al. (1981) described Bechleja rostrata from the Green River Formation, U.S.A.; this and the present redescription of Propalaemon should help to fill in some of the missing information. The following are the main differences between these two genera. Bechleja, according to Houša (1956), has a single filament antennule; Feldmann et al., however, suggest there are two, whereas Propalaemon has three filaments. The main differences according to Houša (1956) are that the telson and uropods of Propalaemon are proportionately larger.

Houša (1956) also states that *Palaemon exul* Frič should not be included in the genus *Palaemon*, 'because it differs from it by several important characters' which he did not clarify. According to Glaessner (1969) the generic diagnosis for *Palaemon* is: 'carapace with antennal and branchiostegal spines; no hepatic spines; antennules three flagellate; telson with four apical spines'. Comparing this with the description by Frič (1872), wherein no mention is made of either antennal or branchiostegal spines, the antennules have two flagellae and the telson lacks apical spines. In addition the fifth pair of pereiopods are stronger and twice the length of the previous pair. Additional well preserved material will undoubtedly support the opinion of Houša (1956) that a new genus is required for *Palaemon exul* Frič.

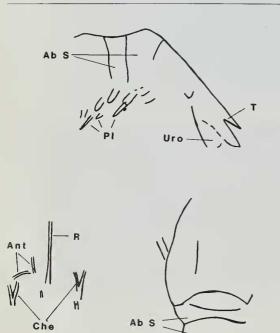
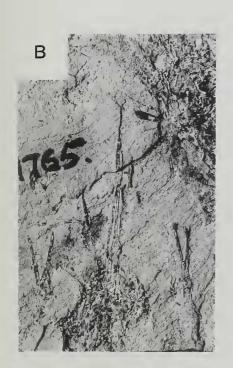


Fig. 3 Propalaemon osborniensis Woodward. A, telson, uropods, somites with incomplete pleonites, In.61690 (×2·3). B, chelae of the second pereiopods, In.61765 (×2). C, incomplete carapace and parts of first two somites, preserved in a dorsoventral view, In.61689 (×2·5).







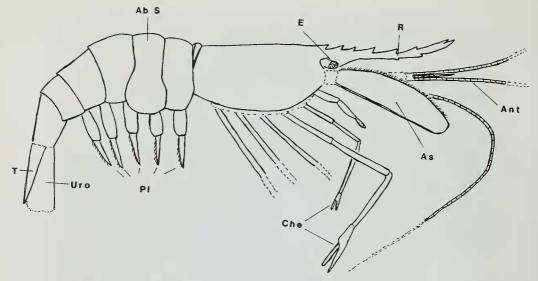


Fig. 4 Propalaemon osborniensis Woodward. Restoration in right lateral view.

Systematic description: Fishes

J. Gaudant

Order AMIIFORMES Huxley, 1861

Family AMIIDAE Bonaparte, 1832

Genus AMIA Linné, 1766

Amia (?) sp.

Newton (1899) distinguished two species, A. anglica Newton and A. colenutti Newton, among the isolated amiid remains found in the Chapelcorner Fish Bed. To the first species are referred isolated vertebrae and scales, one premaxillary and several dermal head bones, while a maxillary found in Colenutt's bed 5 is A. colenutti. However, it is to be noted here that only three scales figured by Newton (1899: pl. 1, figs 19–21) come from Colenutt's bed 3. From the same bed an isolated amiid scale (BMNH P.59773) and an amiid vertebra (found by Mr Kemp of Gosport) have been found recently.

It is not our purpose to give here a taxonomic reassessment of the amiid remains found in the Palaeogene of the Isle of Wight, as it is clear that the scales and the unique vertebra found in Colenutt's bed 3 to date do not allow specific determination. The isolated abdominal vertebra found by Mr Kemp has a typically ovoid sectional outline, but as it probably comes from the middle part of the abdominal region, it is not particularly significant taxonomically.

Order CLUPEIFORMES Bleeker, 1859 Suborder CLUPEOIDEI Bleeker, 1859 Family CLUPEIDAE Cuvier, 1817 Genus VECTICHTHYS nov.

DIAGNOSIS. Differs from other clupeoid genera by the following combination of characters: double-armoured herrings with a complete series of ovoid dorsal scutes, each provided with a median longitudinal crest. Two supramaxillaries. Dentary edentulous. Vertebral column relatively short (about 40 vertebrae). Caudal axial skeleton with first preural (PU1) and anterior ural (U1) centra separate.

Type species. Vectichthys vectensis (Newton).

NAME. From Vectis, the Latin name of the Isle of Wight.

Vectichthys vectensis (Newton 1889) Figs 5-12

1889 Clupea vectensis Newton: 112; pl. 4.

1901 Diplomystus vectensis (Newton) A. S. Woodward: 146.

1982b 'Clupea' vectensis Newton; Grande: 14.

NEOTYPE. All the material figured by Newton (1889) must be considered lost (see note, p. 17). So, the specimen BMNH P.62097 is here designated as neotype of *V. vectensis* (Newton).

MATERIAL. BMNH P.5930, P.6853, P.6853a-h, j-n, P.6854, P.39302, P.59770-2, P.59777-83, P.59789-96 and P.59798-800; BGS GSM 3131 and GSM 97123-30; SMC C.23604-21, C.23624-31, C.23634-47; UMMG 5562a-e; IWCGM 3242.

DIAGNOSIS (emended). Small species, the total length of which does not generally exceed 60 mm. Body slender: maximum height included 4 or $4\frac{1}{2}$ times in standard length. Head large, its length being about a quarter of standard length or slightly more. Upper jaw toothed, maxillary broad, mandible edentulous, dentary projected upwards. Vertebrae 40–41: abdominal 24–25, postabdominal 15–16. Ribs about 20 pairs. Dorsal fin inserted in middle of body, ii – iii + I + 12 rays. Anal fin low, ii – I + 14 – 17 rays. Pectorals moderate in size, with about 10 rays. Pelvic fins relatively small, inserted opposite the origin of dorsal fin and containing seven rays. Eight or nine ovoid dorsal scutes, each with a short median crest. Abdominal scutes not serrated, decreasing in size backwards.

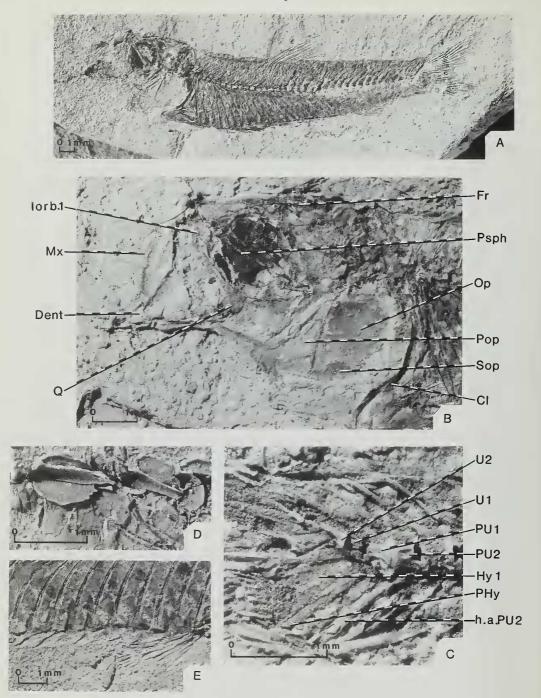
DESCRIPTION. Vectichthys vectensis (Newton) is a small species, the total length generally less than 60 mm. (Newton, 1889, described four large specimens between 43 and 58 mm long, while an incomplete specimen collected by one of us [W.J.Q.] is calculated to have had a standard length of 62 mm.) Moreover, two large, poorly preserved fragmentary fishes (one of them with counterpart), the standard length of which must have been about 220 mm, have also been found recently (P.59798–800): identification of these specimens as this species is not however completely certain.

The head is large, being equal to 25–30% of the standard length. The caudal fin is deeply forked and is always shorter than the head; its length is about equal to the maximum depth of body. The dorsal fin is inserted midway along the body or just in front of this level. It lies opposite the pelvic fins which are inserted midway between the pectoral fins and the origin of the anal fin.

Measurements of several well-preserved specimens are on file in the Department of Palaeontology of the British Museum (Natural History).

The head (Figs 5B, 6) is fairly well preserved in P.6853. It is deep, its height being about three-quarters of its length. Little is known of the anatomy of the cranial roof but the well developed frontals are well exposed, extending beyond the posterior edge of the orbit. A temporal fossa is present (P.59793). The orbit is large, the diameter being almost a third of head length. It is surrounded posteriorly and ventrally by the infraorbital series in which only the large lachrymal carrying the infraorbital canal is clearly seen. However, the position of the posterior components of the infraorbital series seems to indicate a recessus lateralis into which converge the preopercular, the supraorbital and the infraorbital canals.

The mouth is moderately large, the articulation of the lower jaw occurring beneath the middle part of orbit. The mandible (Figs 6, 7) is well developed and massive: its length is included slightly more than twice in the head length while its maximum height reaches almost half of its length. From the symphysis, the relatively low, toothless, oral edge of the dentary rises rapidly towards the coronoid process, which points sharply upwards (P.6853e, P.62097). The upper jaw (Fig. 8) is composed of a relatively small, elongate, toothed premaxilla, the oral edge of which constitutes less than half the jaw (P.59780). The maxilla is robust and has a



convex oral edge on which small denticulations are present (P.59778). Two supramaxillae are present. The first one, which is rod-like (P.59792), is bordered dorsally by the anterior process of the second one, the hind part of which is expanded (P.6853c).

In the palatoquadrate, the quadrate (Fig. 6, Q) is generally well preserved. As usual, it is triangular in shape and its dorsal side is depressed posteriorly to receive the symplectic. The ectopterygoid displays a typical boomerang shape with two arms, the anterior one being prolonged forwards by the dermopalatine (P.59782). The entopterygoid (Enpt) can also be recognized on P.6853c.

The opercular apparatus is characterized by the large size of the operculum. This bone (Fig. 9A) has a typical posterior outline which is concave between its upper part and its posterior angle. A more or less similar concavity of the posterodorsal edge of the operculum is also present in *Knightia* and *Gosiutichthys* described by Grande (1982b).

The rectangular-shaped suboperculum is comparatively small. Its size roughly equals that of the interoperculum. The preoperculum (Fig. 9B) is well developed: its lower arm is almost as long as the vertical one, with which it makes an angle of 110° measured along the two parts of the preopercular canal.

The vertebral column is composed of 40-41 vertebrae, 15-16 of which are postabdominal. This number is slightly more than that of *K. eocaena* Jordan (13-15: Grande 1980) while the number of abdominal vertebrae (23-25) may be compared to that known in *K. alta* (Leidy).

All vertebral centra are elongated. They bear long, slender neural and haemal spines, the distal ends of which reach about two-thirds of the distance from the dorsal (or ventral) part of each centrum to the dorsal (or ventral) margin of the body. In front of the dorsal fin, nine slender predorsal bones are present (P.59793).

Epineurals can be seen along the vertebral column while ventral intermusculars are restricted to the postabdominal region. There are about 20 pairs of long, robust ribs. Excepting the last pair all reach the ventral mid-line. In front of the pelvic fins, the abdomen is provided with a series of about 15–16 abdominal scutes of clupeid type, five or six occurring in front of the origin of the pectoral fins. About nine scutes are present between pelvic and anal fins.

In front of the dorsal fin, another series of eight or nine scutes can be observed (following Grande, 1982b, about 13 scutes would be present). These dorsal scutes (Fig. 10B) are similar to those of the North American species of *Knightia*. They are ovoid with the anterior part slightly drawn out, while their posterior edge is regularly rounded. They are provided with a longitudinal keel, the anterior end of which projects forwards. The shape of these dorsal scutes does not differ significantly from that of similar elements in *K. eocaena* Jordan (as demonstrated by specimen P.4929, Fig. 10A). The same is true for the dorsal scutes of the Recent Australian pellonuline species *Hyperlophus vittatus* (Castelnau) (Fig. 10C; see also Grande, 1982a, figs 25–28), and the clupeines *Gosiutichthys* Grande (1982b: fig. 18), *Herklotsichthys*, *Opisthonema* and *Harengula*.

The caudal fin is deeply forked, the length of the innermost principal rays being no more than half the length of the longest ray of each lobe. Ten principal rays (nine of which are both articulated and branched) are present in the dorsal lobe, while nine principal rays (eight of which are both articulated and branched) make up the ventral lobe. In large specimens (P.59798), the segments of the unbranched principal ray of the dorsal lobe of the caudal fin exhibits a typical zigzag shape. It is to be noted that the inner ray of each lobe is inserted more anteriorly than the principal caudal ray, as in most clupeoids. Dorsally and ventrally, six or seven short marginal (procurrent) rays are present. Each series is preceded by a long rod-like scute.

Specimen P.6853 (Fig. 11A) exhibits five preural vertebrae involved in support of the caudal fin rays. Except for the posterior preural centrum (PU1) which bears a short flat neural arch

Fig. 5 Vectichthys vectensis (Newton). A, general view of the neotype, here designated, P.62097 (×4). B, head of specimen P.6853 (×12), see also Fig. 11A. C, axial caudal skeleton of one of the specimens preserved on the slab P.6854 (×27), see also Fig. 11B. D, dorsal scutes of P.59772 (×20). E, pelvic fin and ventral scutes of P.6853b (×8).

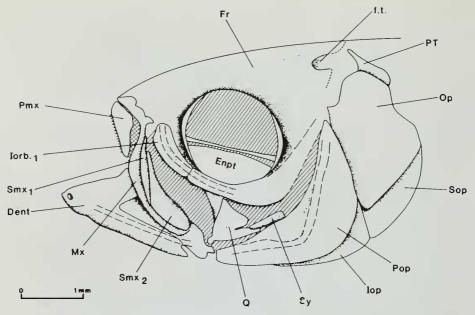


Fig. 6 Vectichthys vectensis (Newton). Reconstruction of the head.

(n.a.PU1), they have elongate neural and haemal spines. The neural and haemal spines of PU4 and PU5 bear the dorsal and ventral rod-like caudal scutes.

One of the fishes preserved on the slab registered P.6854 (Figs 5C, 11B) clearly demonstrates that the end of the vertebral column is composed of three modified vertebrae. The least modified is PU1, with which articulates ventrally a narrow parhypural (PHy). The well-developed U1 is followed by a small triangular element which can be interpreted as a second centrum, U2.

As previously noted by Greenwood (1968) in the fossil genera *Knightia* Jordan and *Diplomystus* Cope, the structure of the caudal skeleton described above, in which PU1 and U1 remain separate, is like that known in Recent double-armoured herrings.

Posteriorly, three elongate, rod-like uroneurals (Un1, Un2, Un3) can be distinguished on specimen P.59792 (Fig. 11C). The first one seems to originate on the posterior preural centrum (PU1), as shown by P.6853 (Fig. 11A). The second originates beneath the preceding one, and a third uroneural is also present posteriorly, just above the upper hypural (Fig. 11C).

The two ural centra support six hypurals. The lower one (Hy 1) is by far the broadest. Its proximal end is somewhat pointed and articulates with the ventral part of U1. The second

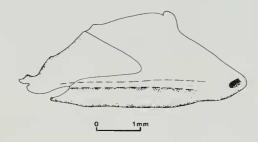


Fig. 7 Vectichthys vectensis (Newton). Right lower jaw of P.59779 in lateral view.

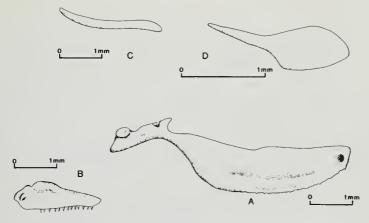


Fig. 8 Vectichthys vectensis (Newton). Components of the upper jaw. A, right maxilla (P.59778) in medial view; B, right premaxilla (P.59780) in medial view; C, anterior supramaxilla (P.59792), see also Fig. 11C; D, posterior supramaxilla (P.6853c).

hypural (Hy 2), long and narrow, is fused with the anterior ural centrum (U1). Hypurals 3 to 6 support the upper lobe of the caudal fin. The lowermost (Hy 3) is the widest. Dorsally, PU1 bears a short neural arch (n.a.PU1). Three epurals (Ep 1–3) occur behind the neural arch of PU1 (Fig. 11A, C).

The dorsal fin includes 15 or 16 rays (Newton, 1889, estimated 14 or 15). The first two (rarely three) are short and they are followed by a long articulated ray which is the longest of the fin; its length is about two-thirds of maximum body height. Posteriorly, 12 articulated and branched rays are present. The dorsal fin rays are generally supported by 13 or 14 rod-like pterygiophores which are relatively short, as only the proximal end of the first reaches the distal part of corresponding neural spines.

The anal fin is of moderate size, comprising 16 to 20 fin rays. The first two are short while the third one, which is articulated but not branched, is the longest of the fin. Its length is slightly less than half the maximum height of the body. Posteriorly, there are 14–17 articulated and branched rays. The endoskeleton of the anal fin has 15–18 (occasionally 19) short, rod-like

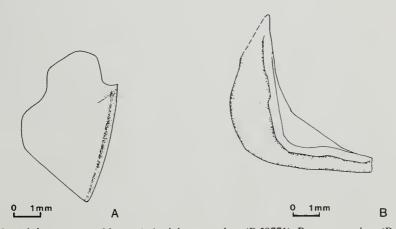


Fig. 9 Vectichthys vectensis (Newton). A, right operculum (P.59771); B, preoperculum (P.59790).

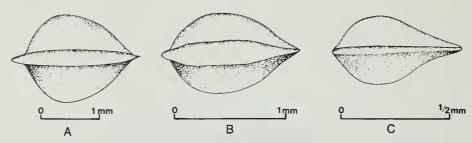


Fig. 10 Dorsal scutes of double armoured herrings. A, Knightia eocaena Jordan (P.4929). B, Vectichthys vectensis (Newton) (P.59772). C, Hyperlophus vittatus (Castelnau). Recent, Australia.

pterygiophores, the proximal ends of which do not reach the distal part of the vertebral haemal spines.

Both the pectoral fins and girdle are imperfectly known. The pectoral fins are of moderate size and contain about ten rays. The cleithrum is generally well preserved. It is characterized by its large vertical arm and its relatively shorter lower arm. The supracleithrum is somewhat slender and articulates dorsally with the bifid post-temporal, the dorsal arm of which is longer than the ventral one.

The pelvic fins are relatively small. Each contains seven rays (Newton, 1889, counted eight or nine rays but this number is clearly inaccurate). They originate midway between the pectorals and the origin of the anal. Their length is equal to about half the distance between their base and the origin of the anal. The pelvic bones are rather slender. Their length is about half that of the fin-rays.

The body is covered with large cycloid scales marked with many circuli which show a largely vertical orientation, characteristic of clupeiform scales. There appear to be about 60–80 circuli per mm (P.59779). As noted by Newton, the lateral line is absent as in all clupeoids. There are about 40 vertical scale rows between the pectoral girdle and the base of the caudal fin. Between the dorsal and pelvic fins about eight longitudinal scale rows may be counted.

RELATIONSHIPS. After its description by Newton (1889), Clupea vectensis was transferred by A. S. Woodward (1901) to the genus Diplomystus Cope. However, Jordan (1907) noted that Cope (1884) had earlier distinguished two sections within his genus Diplomystus. Jordan therefore proposed these sections of Diplomystus should each be considered a distinct genus, and that the generic name Knightia should be used for species having dorsal scutes 'not wider than long' and bearing 'a single median posterior tooth at the end of a median longitudinal carina'. The name Diplomystus Cope (s. str.) was restricted to fishes with 'dorsal scutes . . . transverse with pectinate borders, a median tooth being especially prominent'. So it appears that the clupeid fishes from the Isle of Wight described in this paper are more closely related to Knightia than to Diplomystus, as these fishes have a complete series of more or less ovoid dorsal scutes.

Recently, Grande (1982b) has revised the North American species of *Knightia* Jordan and erected a new allied genus, *Gosiutichthys*. It is thus now possible to use precise data in comparing 'Clupea' vectensis with these fishes. Grande defines the genus *Knightia* as a double-armoured herring with only one supramaxillary bone, 36–40 vertebrae, 20–22 pairs of pleural ribs and 12–14 ovate to circular dorsal scutes. *Gosiutichthys* Grande differs from *Knightia* Jordan in that it has two supramaxillaries and fewer vertebrae (34–36).

Like the North American fossil double-armoured herrings, 'Clupea' vectensis Newton exhibits clupeoid characters in the fusion of the first uroneural with the first preural centrum and the lack of a lateral line. However, as exhibited by the specimen P.6854, the first ural centrum seems to have been larger than in the three North American species of Knightia. Moreover, 'Clupea' vectensis Newton differs from them as it has two supramaxillaries, an edentulous dentary and fewer dorsal scutes (8-9 against 10-14). The English fossil herring differs also from Gosiutichthys Grande in its meristic characters: it has more vertebrae (40-41 against 34-36),

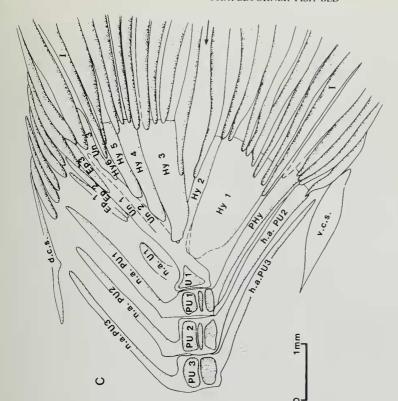
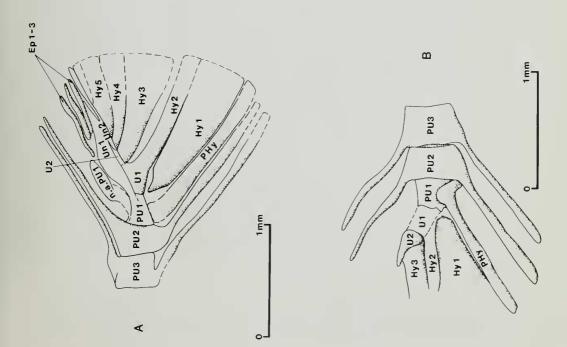
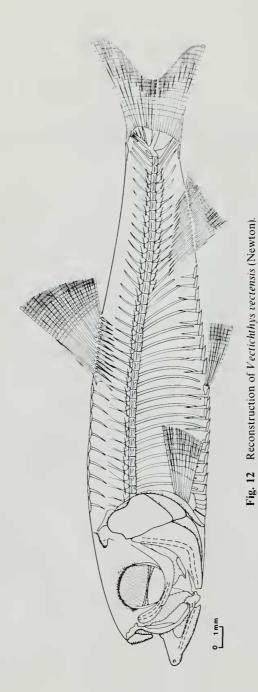


Fig. 11 Axial caudal skeleton of Vectichthys vectensis (Newton). A, P.6853; B, P.6854; C, P.59792: in this specimen the anterior parts of the uroneurals have broken so it is impossible to determine their precise relationships to the ural and preural centra.





more principal dorsal and anal fin rays (respectively 12 and 14–17 against 9–10 and 11) and fewer dorsal scutes (8–9 against 10–13). Anatomical differences can also be noted, as *Gosiutichthys* has small conical teeth on the dentary and a more slender posterior supramaxillary.

On the other hand, Grande (1982b) suggests that 'Knightia' brasiliensis Woodward, from the Cenozoic of Maranhão (Brazil), might be congeneric with 'Clupea' vectensis Newton. In the present state of knowledge, this suggestion does not seem to be sufficiently founded, as Grande himself notes that the anatomy of the Brazilian species is still imperfectly known; it is not possible to determine either the shape of its dorsal scutes or the number of supramaxillary bones.

Finally, as demonstrated by Grande (1982a), *Ellimma branneri* (Jordan), from the Alagôas series (? Upper Eocene) of Riacho Doce (Brazil), which was considered by Schaeffer (1947) to belong to *Knightia* Jordan, must be left aside in a separate genus as it has two supramaxillaries (Grande 1982b: fig. 19) and ornamented dorsal scutes (Grande 1982a: fig. 23).

So, if we make reference to the diagnoses of *Knightia* Jordan, *Gosiutichthys* Grande and *Ellimma* Jordan, the double-armoured clupeid from the Isle of Wight does not belong to any of these genera. For this reason, the species initially described as *Clupea vectensis* Newton must be considered the type-species of a new, currently monotypic, genus here named *Vectichthys*, the diagnosis of which is given on p. 22.

It is relatively difficult to determine the precise systematic position of *Vectichthys* within the Clupeidae. According to Grande (1985), five subfamilies may be recognized in this family (Dussumieriinae and Spratelloidinae included). As shown by Grande (1982a, 1985), fishes with dorsal scutes are known in most of them. In many species only one dorsal scute is present. But in others, such as *Clupanodon thrissa* (Lacépède) (Dorosomatinae), *Ethmidium maculatum* (Valenciennes) (Alosinae), *Gosiutichthys parvus* (Grande) and *Ellimma branneri* (Jordan) (Clupeinae) and several Pellonulinae (*Hyperlophus*, *Potamolosa* and *Knightia eocaena* Jordan), there is an extended series between the skull and the dorsal fin. Among these forms with many dorsal scutes those of *Vectichthys* appear to match the circular to oval type found in the pellonuline genera. Grande (1982a: 30) ranks dorsal scutes of this shape as derived within clupeid fishes and if this is so it may be taken as evidence of pellonuline affinites for *Vectichthys*. The caveat to this view is that a single dorsal scute of similar shape is also found in the clupeines *Herklotsichthys*, *Opisthonema*, *Sardinella* and *Gosiutichthys* (Grande 1982b), and in some *Alosa* spp. (Grande 1982a).

The Pellonulinae, as characterized by Grande (1985), are recognized by the absence of an anterior supramaxilla, which suggests *Vectichthys* is more plesiomorphic in this respect. Furthermore, the assumed more plesiomorphic pellonulines (*Potamolosa*, *Hyperlophus*, *Clupeoides* and *Sierrathrissa*—Grande 1985: fig. 21) show separate PU1 and U1, like *Vectichthys*. Thus, *Vectichthys* might be considered as the most plesiomorphic pellonuline, showing a continuous series of ovoid dorsal scutes but lacking specializations in the caudal skeleton and the supramaxillary series. *Gosiutichthys* is very similar to *Vectichthys* in these respects but retains two supramaxillary bones and is provisionally considered as a clupeine by Grande (1982b).

Order PERCIFORMES Bleeker, 1859
Suborder GOBIOIDEI Berg, 1940
Family GOBIIDAE Bonaparte, 1831
Genus POMATOSCHISTUS Gill, 1864

Pomatoschistus (?) cf. bleicheri (Sauvage, 1883) Figs 13-16

1979 Gobius: Ford: 109.

MATERIAL. The occurrence of fossil gobiids in the Chapelcorner Fish Bed was reported first by Ford (1979). His collection included one small fish which we were able to identify as a representative of this family, during a short visit to Yarmouth (May, 1977). Several other specimens

(BMNH P.59774-7, P.59784-8 and P.59797) have been collected subsequently at King's Quay. Moreover, two small gobiids have been recognized among the clupeids from the Chapelcorner Fish Bed kept in the Sedgwick Museum (C.23632-3).

DESCRIPTION. The gobiids from the Chapelcorner Fish Bed are small, elongate fishes, the standard length of which does not exceed 35 mm. The height of the body is about one-fifth or one-sixth of standard length. The head is large, its length being included about 3 or $3\frac{1}{2}$ times in the standard length. The caudal fin is rounded and is only one-sixth of standard length. The caudal peduncle is elongate: its length equals about $2\frac{1}{2}$ times its width. The main measurements of the two complete specimens are on file in the Department of Palaeontology, British Museum (Natural History).

P.59786 is a well-preserved small specimen, the head of which is crushed dorsoventrally. Both frontals (Fr) are clearly exposed. Their supraorbital part, which is relatively broad, is delimited laterally by a regularly rounded orbital edge. In front of the frontals, the mesethmoid is partially preserved. The hind part of the skull roof exhibits the supraoccipital, somewhat displaced. The dermopterotic can also be recognized.

In the upper jaw, the premaxillary (Pmx) is large. Its toothed oral process constitutes the

entire oral edge of the jaw.

The lower jaw is well exposed on specimen P.59784 (Fig. 14), where its two rami are still in connection. The angular and the dentary can be recognized. Moreover, an isolated dentary is also preserved on slab P.59775. The oral edge is provided with small conical teeth and rises gently backwards before ending in a rounded coronoid process. The quadrate (Q) is triangular and shows a posterior furrow into which fits the symplectic (Sy). Anteriorly, the ectopterygoid (Ecpt) lies in front of the quadrate. It is overlapped by the rod-like entopterygoid (Enpt). The preoperculum (Pop) has two arms, the lower of which is the longer. The operculum (Op) is triangular and has a convex upper edge. It is covered with cycloid scales. Beneath the operculum, the suboperculum (Sop) is relatively narrow.

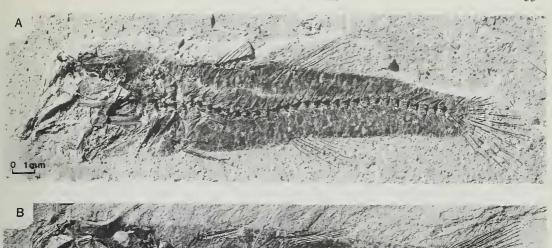
Of the hyoid arch, the hyomandibular, which has a very massive proximal part, can be seen on specimen C.23632. The symplectic tapers regularly towards the distal end, as shown by P.59784 on which a posterior ceratohyal (Chy 2) is also preserved. This bone has a widened

proximal part. It bears six narrow, needle-like branchiostegal rays (R br.).

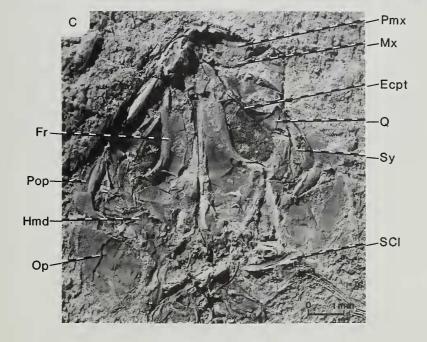
The vertebral column contains about 30 vertebrae: 12 abdominal and 18 postabdominal. The vertebral centra are elongate and constricted midway along their length. The neural and haemal spines of postabdominal vertebrae are moderately elongate as their distal ends reach only about two-thirds of the distance between the dorsal (or ventral) part of the vertebral centra and the dorsal (or ventral) mid-line of body. The last three postabdominal vertebrae constitute the endoskeleton of the caudal fin with their enlarged haemal and neural spines. The ribs are relatively short and slender and are borne by strong parapophyses, more strongly developed in the hind part of the abdominal region. There are about 10 pairs of ribs.

The margin of the caudal fin is either more or less convex or truncated, as shown by P.59784 in which 12 principal fin-rays, both articulated and branched, can be counted. In front of these about 12 short marginal (procurrent) rays are present, both dorsally and ventrally. The caudal fin rays are supported by three vertebrae: two preural ones (PU_2 and PU_3) and the uroterminal complex ($PU_1 + U_1$), fused with the triangular dorsal hypural plate ($PU_3 + PU_4$) (Fig. 15). There is a narrow, rod-like upper hypural (PU_3), while the large triangular lower hypural plate (PU_3) articulates with the ventral part of the uro-terminal complex. The parhypural (PU_3) originates immediately in front of the lower hypural plate. Dorsally, one epural (PU_3) is present. In front of this, the posterior free preural centrum (PU_3) bears a short neurapophysis, while the corresponding haemapophysis is normally developed, as are the apophyses borne by PU_3 .

Fig. 13 Pomatoschistus (?) cf. bleicheri (Sauvage), Chapelcorner Fish Bed, King's Quay, Isle of Wight. A, general view of P.59785 (×6). B, general view of P.59784 (×4); see also Figs 14–15. C, head of P.59786 (×10).







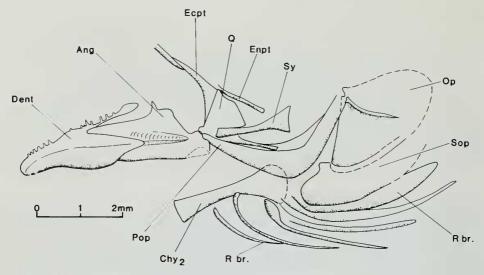


Fig. 14 Pomatoschistus (?) cf. bleicheri (Sauvage). Partial view of the cheek (P.59784).

The anterior dorsal fin originates in front of the middle of the body. It comprises six or sometimes seven short, slender spines, the distal ends of which do not reach the beginning of the posterior dorsal fin. The second or third spine is the longest; its length equals about two-thirds of the distance between the origin of the two dorsal fins. The endoskeleton of the anterior dorsal fin is composed of six or seven rod-like pterygiophores.

The posterior dorsal fin is situated in the posterior half of the body. It is composed of a short slender spine and nine or ten articulated rays; the first one is unbranched. This ray is the longest of the fin, equal in length to about 0.7 or 0.8 of the maximum height of the body, while the other rays are progressively shorter backwards. The endoskeleton consists of 10 or 11 rod-like pterygiophores.

The anal fin is exactly opposed to the posterior dorsal; it begins precisely under the origin of this fin or slightly behind it. It is composed of one short slender spine and eight or nine articulated rays (of which only the first one is unbranched). The length of the anal fin is slightly less than that of the posterior dorsal. The endoskeleton comprises about 10 pterygiophores.

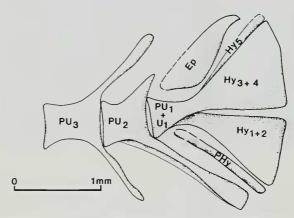


Fig. 15 Pomatoschistus (?) cf. bleicheri (Sauvage). Axial caudal skeleton (P.59784).

The pectoral girdle remains poorly known. The cleithrum is partly preserved on specimens P.59784–5. An elongate, dorsally tapering supracleithrum is exposed on P.59786, while a forked post-temporal is present on P.59785. The endoskeletal bones of the pectoral girdle are not preserved, although P.59787 shows enlarged radials. The pectoral fins are inserted in the lower third of the flank, and comprise about 14 rays of moderate length.

The pelvic fins are situated just under and slightly in front of the pectorals. They consist of one short slender spine and five rays. It is not known if the pelvic fins were united as in Recent gobiid fishes (sensu Regan 1911).

The body as seen in P.59786 is covered with ctenoid scales, the free edge of which is ornamented with a series of small spines. In medial view, the scale surface is covered with a series of longitudinal, more or less winding lines. As pointed out earlier, cycloid scales, showing regularly concentric circuli, are present on the head (especially on the operculum of P.59786).

RELATIONSHIPS. It is always difficult to make precise taxonomic determination of fossil gobiid fishes. In fact, to distinguish Recent genera of this family, ichthyologists use soft anatomical characters of the cephalic sensory system which are, of course, not preserved in fossils. For this reason, it may seem more simple to consider fossil gobiid species as members of the genus *Gobius* L. (s.l.). However, several meristic and morphometric characters of the gobiids described in this paper allow a comparison with the Recent genus *Pomatoschistus* Gill. In fact, the number of vertebrae and the construction of the unpaired fins in the fossil gobiid from the Chapelcorner Fish Bed do not differ significantly from those exhibited by several Recent species of *Pomatoschistus* Gill, especially *P. minutus* (Pallas) and *P. canestrini* (Ninni). For example, it may be noted that, like *P. minutus*, the present fossil gobiid sometimes has seven spines in the anterior dorsal fin. Another character, the occurrence of a long and slender caudal peduncle, also suggests a comparison between it and the Recent species of *Pomatoschistus* Gill.

If these meristic and morphometric characters are sufficient to allocate the Isle of Wight fossil gobiid to the genus *Pomatoschistus* Gill, it still remains to determine its probable relationship to other species belonging to this genus. Among the Recent species, the greatest similarity is to be found with *P. canestrini*, the unpaired fins of which are very similar to those of the fossil gobiid. However, it must be noted that *P. canestrini* (Ninni) never has seven spines in the anterior dorsal fin. This is a feature of *P. minutus* which, otherwise, has 10–12 rays in both the posterior dorsal and the anal fins (Tortonese 1975).

A comparison of the gobiid from the Fish Bed with a fossil species from the Lower Oligocene of Alsace, recently considered as probably belonging to *Pomatoschistus* Gill (Gaudant 1979), shows that no significant difference exists between them. Recently, new specimens of *P. bleicheri* (Sauvage) (first described as *Paralates bleicheri* Sauvage 1883: 485) have been collected from Strangenberg quarry, near Rouffach, which provide more information concerning this species. The diagnosis given earlier (Gaudant 1979) must be slightly emended as the number of postabdominal vertebrae can be 17 or 18 (not just 17), while the number of soft rays of the posterior dorsal fin is nine or ten (not just ten). These small modifications of the diagnosis of *Pomatoschistus bleicheri* leave no significant meristic or morphometric difference between it and the gobiid in the Chapelcorner Fish Bed. For this reason, we consider that the fossil gobiid from the Isle of Wight may belong to, or is very close to, *P. bleicheri*. However, it must be emphasized that the assignment of this species to the Recent genus *Pomatoschistus* remains provisional, as already noted for the material from Rouffach (Gaudant 1979).

Interpretation of Palaeoenvironment

The fossil content of the grey-bluish shaly clay generally known as the Chapelcorner Fish Bed includes a palaemonid prawn (*Propalaemon osborniensis*) and three fish species: *Amia* (?) sp., *Vectichthys vectensis* and *Pomatoschistus* (?) cf. *bleicheri*. This fossil association and the mode of fossilization of each species are very significant and may be used for determining the conditions of deposition of the Chapelcorner Fish Bed.

Except for the amiid remains, which are exclusively isolated bones and scales, all other fossils collected are articulated skeletons. This could indicate that the amiid remains were washed in

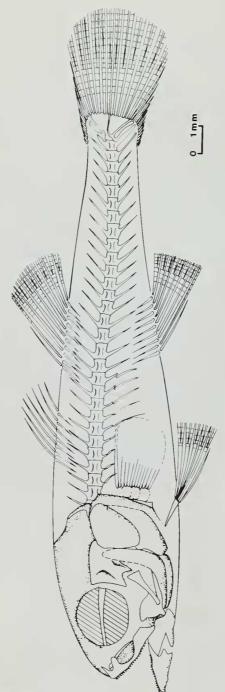


Fig. 16 Reconstruction of Pomatoschistus (?) cf. bleicheri (Sauvage).

while other animals were living in the area of deposition of the fossiliferous clay. If taken separately, the three animal species here considered as autochthonous do not clearly characterize any precise type of palaeoenvironment. In fact, all belong to euryhaline families, able to live in sea, brackish or fresh water.

Palaemonid prawns belonging to the subfamily Palaemoninae are now living in these three types of environments throughout the world (America, Europe, west Africa, Mediterranean, Indo-Pacific region). For example, the genus *Leander* Desmarest, with about 50 species, is mainly distributed in sea-water but has several fresh-water species, while *Palaemonetes* Heller, with 15 species, lives mainly in estuaries or in brackish water, but is also represented in fresh water. Conversely, *Palaemon* Weber has about 75 species and is mainly fresh-water, although some of them are also present in estuaries (Panikkar 1941). In his extensive study of Recent American Palaemoninae, Holthuis (1952) has shown that these prawns live in every type of aquatic environment (marine, estuarine, lagoonal, fresh-water and even subterranean waters).

Among fossil Cenozoic palaemonids found in Europe and North America, several species ('Palaemon' exul Fric and Bechleja inopinata Housa, from the Oligocene of Kučlín; Micropsalis papyracea von Meyer, from the Upper Oligocene of Rott; Homelys minor von Meyer, from the Middle Miocene of Öhningen) are considered to have lived in fresh water. The same seems to have been true for the North American species Bechleja rostrata Feldmann, Grande & McCoy, recently described in the F 2 unit of the Green River Formation, in which it is associated with fresh-water fishes such as moon-eyes (Eohiodon falcatus Grande), gars (Lepisosteus simplex (Leidy)) and stingrays (Heliobatis radians Marsh).

Recent double-armoured representatives of the subfamily Pellonulinae live exclusively in Australasia (*Hyperlophus* Ogilby and *Potamalosa* Ogilby), where they either inhabit fresh water (*Potamalosa*) or are diadromous (*Hyperlophus*).

The occurrence of a gobiid—tentatively referred to the genus *Pomatoschistus*—is no more indicative of the salinity. In fact, although they belong to a primarily marine family, some Recent gobiids are exclusively fresh-water as, for example, the two Italian species *G. nigricans* Canestrini and *Padogobius martensi* (Günther) (Gandolfi & Tongiorgi 1974). Moreover, at least two European species of *Pomatoschistus* (*P. minutus* (Pallas) and *P. canestrini* (Ninni)) are euryhaline. *P. canestrini* has fresh-water populations living in a Jugoslavian river (Ladiges & Vogt 1965).

In conclusion, it is only possible to suggest that the autochthonous fishes and crustaceans found in the 'Chapelcorner Fish Bed' are all more or less euryhaline organisms, which seem to indicate a brackish water palaeoenvironment in which no exclusively marine animal was able to live. The presence of scattered remains of *Amia* may be explained by suggesting that they lived in rivers flooding towards the lagoon in which deposition of the fossiliferous clay took place.

The palaeoclimatic information provided by fossils found in the Chapelcorner Fish Bed is somewhat imprecise. Palaemonid prawns are cosmopolitan and the generic assignment of the gobiids is only provisional. Nevertheless, *Vectichthys* stands very near the Recent 'Hyperlophini' which inhabit Australian waters in which palaemonid prawns also live. This may suggest that during the deposition of the fossiliferous clay the climate was relatively hot and humid, like that of Recent tropical or subtropical regions, as suggested by Daley (1972) for Bembridge Marl times. However, information provided by the fossil content of the Chapelcorner Fish Bed is still too scanty to allow a sound palaeoclimatic interpretation.

Acknowledgements

Grateful thanks are due to Mr J. S. H. Collins, Dr L. Grande, Dr P. L. Forey and Mr S. F. Morris for reading parts of the manuscript and suggesting helpful changes. Mr R. L. E. Ford (Yarmouth) is warmly acknowledged for hospitality and assistance given to the senior author during field work near Wootton Creek (May 1977). For allowing access to material and/or information, we are also indebted to Dr H. W. Ball (BMNH), Dr I. Cooke (British Geological Survey, Keyworth), Mr J. Cooper (BMNH), Dr J. Cooper (Booth Museum of Natural History, Brighton), Dr R. M. C. Eagar (UMMG), Dr G. F. Elliott

(Cirencester), Dr C. L. Forbes (SMC), Dr J. J. Hooker (BMNH), Dr A. Insole (IWCGM), Mr D. J. Kemp (Gosport Museum), Dr C. Patterson (BMNH), Dr H. P. Powell (University Museum, Oxford), Mr D. Rodgers (London) and Dr H. Torrens (University of Keele, Editor of *The Geological Curator*).

This research has been partly supported by grants from the C.N.R.S. and the British Council to the

senior author.

The drawings of the fishes are by Mr J. Dyon and the photographs of them by Mr D. Serrette (Paris).

References

- Cavelier, C. 1979. La limite Eocène-Oligocène en Europe occidentale. Sciences géol. Inst. Géol., Strasbourg, Mém., 54: 1–280.
- Colenutt, G. W. 1888. On a portion of the Osborne beds of the 1sle of Wight, and on some remarkable organic remains recently discovered therein. *Geol. Mag.*, London, (3) 5: 358–362.
- Cope, E. D. 1884. The Vertebrata of the Tertiary formations of the West. Rep. U.S. geol. geogr. Surv. Territ., Washington, 3, 1009 pp., Atlas 75 + pls.
- Daley, B. 1972. Some problems concerning the early Tertiary climate of southern Britain. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, Amsterdam, 11: 177–190.
- Feldmann, R. M., Grande, L., Birkhimer, C. P., Hannibal, J. T. & McCoy, D. L. 1981. Decapod Fauna of the Green River Formation (Eocene) of Wyoming. *J. Paleont.*, Tulsa, 55 (4): 788–799.
- Ford, R. L. E. 1979. A genus of fossil fish new to the Isle of Wight. *Proc. Isle Wight nat. Hist. archaeol. Soc.*, Newport, 7 (for 1977): 109–110.
- Frič, A. 1872. Über *Palaemon exul*, eine neue Crustacee aus dem Polirschiefer von Kutschlin bei Bilin in Böhmen. Sber. K. böhm. Ges. Wiss. Math.-nat. Kl., Prague, 1872: 37–38.
- Gamble, H. J. 1982. Formal introduction of the term 'Chapelcorner Fish Bed', as a revised lithostratigraphical unit within the Osborne Member of the Solent Formation (Upper Eocene; Isle of Wight). Tertiary Res., Leiden, 4 (1): 35–37.
- Gandolfi, G. & Tongiorgi, P. 1974. Taxonomic position, distribution and biology of the gobies present in the Italian freshwaters, *Padogobius martensi* (Günther) and *Gobius nigricans* Canestrini (Osteichthyes, Gobiidae). *Annali Mus. civ. Stor. nat. Giacomo Doria*, Genova, 80: 92–118.
- Gaudant, J. 1979. Sur la présence de Gobiidae (poissons téléostéens) dans l'Oligocène inférieur de Rouffach (Haut-Rhin). Sciences géol. Inst. Géol. Strasbourg, Bull., 32 (3): 131-137, 1 pl.
- Glaessner, M. F. 1929. Crustacea Decapoda. In Pompeckj, F. J. (ed.), Fossilium Catalogus (1: Animalia), pars 41: 1-464. Berlin.
- —— 1969. Decapoda; Addendum to Decapoda. In Moore, R. C. (ed.), Treatise on Invertebrate Paleontology, R (Arthropoda 4, 2): R399-533, R626-628. Lawrence, Kans. & Boulder, Col.
- Grande, L. 1980. Paleontology of the Green River Formation, with a review of the fish fauna. *Bull. geol. Surv. Wyo.*, Laramie, 63. xvii + 333 pp.
- 1982a. A revision of the fossil genus *Diplomystus*, with comments on the interrelationships of clupeomorph fishes. *Am. Mus. Novit.*, New York, 2728: 1–34.
- 1982b. A revision of the fossil genus *Knightia*, with a description of a new genus from the Green River Formation (Teleostei, Clupeidae). *Am. Mus. Novit.*, New York, **2731**: 1–22.
- 1985. Recent and fossil clupcomorph fishes with materials for revision of the subgroups of clupeids. Bull. Am. Mus. nat. Hist., New York, 181 (2); 231–372.
- Greenwood, P. H. 1968. The osteology and relationships of the Denticipitidae, a family of clupeomorph fishes. *Bull. Br. Mus. nat. Hist.*, London, (Zool.) 16: 213–273.
- Holthuis, L. B. 1952. The subfamily Palaemoninae. A general revision of the Palaemonidae (Crustacea, Decapoda, Natantia) of the Americas. II. *Occ. Pap. Allan Hancock Fdn*, Los Angeles, 12: 1–396, pls 1–55.
- Houša, V. 1956. Bechleja inopinata n.g., n.sp., nový ráček z českých třetihor (Decapoda, Palaemonidae). Sb. Ústřed. Úst. Geol., Prague, (Paleont.) 23: 365–377, 3 pls.
- Insole, A. & Daley, B. 1985. A revision of the lithostratigraphical nomenclature of the Late Eocene and Early Oligocene strata of the Hampshire Basin, Southern England. *Tertiary Res.*, Leiden, 7 (3): 67–100.
- **Jordan, D. S.** 1907. The fossil fishes of California with supplementary notes on other species of extinct fishes. *Univ. Calif. Publs Bull. Dep. Geol.*, Berkeley, 5 (7): 95–144, pls 11–12.
- Ladiges, W. & Vogt, D. 1965. Die Süsswasserfische Europas. 250 pp., 44 pls. Hamburg & Berlin.
- Newton, E. T. 1889. Description of a new species of *Clupea (C. vectensis)* from Oligocene strata in the Isle of Wight. Q. Jl geol. Soc. Lond., 45: 112-117, pl. IV.
- —— 1899. On the remains of *Amia* from Oligocene strata in the Isle of Wight. Q. Jl geol. Soc. Lond., 55: 1-10, pl. 1.

- Panikkar, N. K. 1941. Osmoregulation in some palaemonid prawns. J. mar. biol. Ass. U.K., Plymouth, 25: 317–359.
- **Regan, C. T.** 1911. The osteology and classification of the gobioid fishes. *Ann. Mag. nat. Hist.*, London, (8) 8: 729-733.
- Sauvage, H. E. 1883. Notes sur les Poissons Fossiles. XXXI. Sur des poissons du Tongrien de Rouffach (Haute-Alsace). Bull. Soc. géol. Fr., Paris, (3) 11: 483-485.
- Schaeffer, B. 1947. Cretaceous and Tertiary actinopterygian fishes from Brazil. Bull. Am. Mus. nat. Hist., New York, 89: 1–39, pls 1–7.
- Tortonese, E. 1975. Osteichthyes-Pesci ossei (parte secunda). In: Fauna d'Italia, 11. xviii + 636 pp. Bologna.
- Woods, H. 1925. A monograph of the fossil macrurous Crustacea of England. Part I. *Palaeontogr. Soc.* (*Monogr.*), London (for 1922): 1–16, pls 1–4.
- Woodward, A. S. 1901. Catalogue of the fossil Fishes in the British Museum (Natural History), 4. xxxviii + 636 pp., 19 pls. London, British Museum (Natural History).
- Woodward, H. 1903. On some fossil prawns from the Osborne beds of the Isle of Wight. *Geol. Mag.*, London, (4) 10: 97-99, pl. 5.